Structure-dynamic relationship of plant–insect networks along a primary succession gradient on a glacier foreland

Losapio, Gianalberto ; Jordán, Ferenc ; Caccianiga, Marco ; Gobbi, Mauro

Abstract: There is a growing interest in understanding the structure–dynamic relationship of ecological networks. Ecological network changes along primary successions are poorly known: to address such topic, gradient of primary succession on glacier forelands is an ideal model, as sites of different age since deglaciation stand for different ecosystem developmental stages. We aimed to investigate the assembly processes of plant–insect networks and to elucidate its functional implications for ecosystem stability along this time sequence succession. We collected data on the functional role of anthophilous insect groups and performed network analysis to evaluate their relative importance in the structure of plant–insect interaction networks with increasing time since deglaciation along the primary succession of a debris-covered glacier foreland. We sampled anthophilous insects visiting the flowers of two models plant species, Leucanthemopsis alpina and Saxifraga bryoides. Insects were identified and trophic roles were attributed to each taxon (detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists) at five sites representing the primary succession gradient. Plant–insect interactions were visually represented by a bipartite network for each successional stage. For each plant species and insect group, centrality indices were computed quantifying their community importance. For the whole network, centralization and link density were calculated. Pollinators dominated pioneer communities on the debris-covered glacier and in recently deglaciated areas, while parasitoids, predators and opportunists characterised late-succession stages. Plant species centrality varied along the succession. Pollinators showed initially higher but then decreasing centrality, while the centrality of predators and parasitoids increased with time since deglaciation. Along the same gradient link density showed an increasing trend while network centralization tended to decrease. The present study provides new insight into the initial steps of plant–insect network assembly and sheds light on the relationship between structure and dynamic in ecological networks. In particular, during the succession process, more links are formed and plant–anthophilous insect interactions change from a network dominated by pollinators to a functionally more diversified food web. We conclude that applying network theory to the study of primary succession provides a useful framework to investigate the relationship between community structure and ecosystem stability.

DOI: https://doi.org/10.1016/j.ecolmodel.2015.07.014

Originally published at:
Losapio, Gianalberto; Jordán, Ferenc; Caccianiga, Marco; Gobbi, Mauro (2015). Structure-dynamic relationship of plant–insect networks along a primary succession gradient on a glacier foreland. Ecological Modelling, 314:73-79.
DOI: https://doi.org/10.1016/j.ecolmodel.2015.07.014

Structure-dynamic relationship of plant–insect networks along a primary succession gradient on a glacier foreland

Gianalberto Losapio[a,b*], Ferenc Jordán[c,d], Marco Caccianiga[a], Mauro Gobbi[e]

[a] Department of Biosciences, University of Milan, Via Celoria 26, I-20133 Milan, Italy

[b] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[c] The Microsoft Research, University of Trento Centre for Computational and Systems Biology (COSBI), Piazza Manifattura 1, I-38068 Rovereto (TN), Italy

[d] Danube Research Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Karolina 29, H-1113 Budapest, Hungary

[e] Department of Invertebrate Zoology and Hydrobiology, MUSE – Museo delle Scienze, Corso del Lavoro e della Scienza 3, I-38123 Trento, Italy

[*] Corresponding author: gianalberto.losapio@ieu.uzh.ch

ABSTRACT

There is a growing interest in understanding the structure–dynamic relationship of ecological networks. Ecological network changes along primary successions are poorly known: to address such topic, gradient of primary succession on glacier forelands is an ideal model, as sites of different age since deglaciation stand for different ecosystem developmental stages. We aimed to investigate the assembly processes of plant-insect networks and to elucidate its functional implications for ecosystem stability along this time sequence succession. We collected data on the functional role of anthophilous insect groups and performed network analysis to evaluate their relative importance in the structure of plant-insect interaction networks with increasing time since

deglaciation along the primary succession of a debris-covered glacier foreland. We sampled anthophilous insects visiting the flowers of two models plant species, *Leucanthemopsis alpina* and *Saxifraga bryoides*. Insects were identified and trophic roles were attributed to each *taxon* (detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists) at five sites representing the primary succession gradient. Plant-insect interactions were visually represented by a bipartite network for each successional stage. For each plant species and insect group, centrality indices were computed quantifying their community importance. For the whole network, centralization and link density were calculated. Pollinators dominated pioneer communities in recently deglaciated areas, while parasitoids, predators and opportunists characterised late-succession stages. Plant species centrality varied along the succession. Pollinators showed initially higher but then decreasing centrality, while the centrality of predators and parasitoids increased with time since deglaciation. Along the same gradient link density showed an increasing trend while network centralization tended to decrease. The present study provides new insight into the initial steps of plant–insect network assembly and sheds light on the relationship between structure and dynamic in ecological networks. In particular, during the succession process, more links are formed and plant-anthophilous insect interactions change from a network dominated by pollinators to a functionally more diversified food web. We conclude that applying network theory to the study of primary succession provides a useful framework to investigate the relationship between community structure and ecosystem stability.

Keywords: bipartite network, chronosequence, community assembly, ecological network, ecosystem stability

1. Introduction

The study of ecological interaction networks is becoming a key approach for understanding ecological and evolutionary processes (Vázquez et al. 2009) as it provides useful depictions of biodiversity, species interactions, ecosystem structure and functioning (Dunne et al. 2002b). Despite the growing recognition of the importance in analysing the whole-community organization following an ecological network approach (Sridhar et al. 2013), there is still a lack of information on how ecological networks are assembled (Bascompte and Stouffer 2009) and the relationship between ecosystem dynamics and network structure is still poorly understood (Jordán 2009).

Recent researches on network ecology provided new insight into structural invariant patterns underlying species interactions. The organization in connected modules (Olesen et al 2007) with a heterogeneous distribution of the number of interactions per species (Dunne et al. 2002a) and asymmetric interaction strength among species (Bascompte 2009) has been related to ecological network robustness (Pocock et al. 2012) and stability (Thébault and Fontaine 2010). Little attention, however, is given to the spatial aspects and to the temporal dimension of ecological networks, despite their relevance for mechanisms of network formation (Bascompte and Stouffer 2009) and for network robustness to species extinction (Pascual and Dunne 2006).

Ecological succession (i.e. the change of species composition over time) provides temporal and spatial dimensions to analyse the change in the characteristics of populations, communities and ecosystems (Walker & del Moral 2003), and may therefore be suitable to look at the temporal dynamics of ecological networks. Glacier forelands represent such a gradient of primary succession, as sites of different age since deglaciation stand for different ecosystem developmental stages (Matthews 1992).

The use of the chronosequence as a space-for-time substitution (Foster and Tilman 2000) along glacier foreland has provided significant insights into the patterns and mechanisms of plant (Walker et al. 2010) and arthropod (Kaufmann 2001) community assembly. Vegetation cover, plant and

arthropod diversity increase throughout the succession (Hodkinson et al. 2001, Gobbi et al. 2010). Plant community structure changes due to different efficient resource-use among pioneer and late-successional species (Caccianiga et al. 2006). In parallel, the turnover of arthropods is influenced by the stabilization of environmental conditions and vegetation structure (Gobbi et al. 2006). However, previous studies have focused on a single trophic level and very little is known about ecological network assembly during primary succession (Albrecht et al. 2010). The only plant-pollinator network examined along such a gradient showed an increase in interaction diversity and indicated an increase in pollinator diet breadth (Albrecht et al. 2010).

While the majority of ecological network studies examine one static network at a time, we aimed to analyse a network gradient, one of the important perspectives in ecological network analysis. Thus, we applied the network analysis by bipartite network and local to global importance indices analysis to describe the structure of plant-anthophilous insect network and we compared it among different successional stage of a glacier foreland, focusing on insect trophic roles. Thus, we performed network analysis to evaluate the structure of the network and compared it among different successional stages of a glacier foreland. In particular we addressed the following questions: (i) Does the structural importance of plants and insects vary along the successional gradient? (ii) How does the network architecture change along the spatio-temporal gradient? Finally, by integrating structure with dynamic of ecological networks we provide new insight into network assembly and arise empirical models for species coexistence and ecosystem stability.

2. Material and methods

Data sampling

The study was performed along the glacier foreland of Vedretta d'Amola glacier (Central Italian Alps, 46°13'16”N, 10°40'41”E), which is a debris-covered glacier of about 82.1 ha, with two thirds

covered by stony debris with variable depth, from few centimetres to approximately one meter. The glacier foreland is 1.23km long, covers an altitudinal range from 2425m to 2560m a.s.l., and is characterized by a big moraine system dating back to the Little Ice Age (1500-1850 A.D.). Field observations and various sources including maps, reports, aerial photographs, iconography, and records of length change made over the last 100 years allowed the reconstruction of the glacier tongue position during the largest extent reached: at the end of the Little Ice Age (c. 1850 A.D.), in 1925 A.D., and in 1994 A.D (Fig.1). Following this deglaciation gradient five sampling sites were located to represent the main successional stages: glacier surface (stage 0), 1-20 years (stage I), 21-90 years (stage II), 91-160 years (stage III), and more than 160 years (stage IV).

We selected the flowering plants *Leucanthemopsis alpina* (L.) Heyw. (Asteraceae) and *Saxifraga bryoides* L. (Saxifragaceae) as model species because they were the only two entomophilous plant species that occurred throughout the whole primary succession gradient. At each successional stage, two 25 m^2 plots were established and three *L. alpina* tufts and three *S. bryoides* cushions were selected for each species and marked for further use over the course of the study. The number of flowers of each tuft or cushion was recorded in July 2012. Plant-anthophilous insect interactions were observed during the flowering seasons (between the end of July and the end of August) of the summers of 2012 and 2013. All anthophilous insects visiting the flowers were sampled with an entomological aspirator by observing the three plant species units together during three periods of 40 minutes a day at 11am, 1pm and 3pm (90 samples in total per year). Anthophilous insects were identified at species level if possible, otherwise at genus or family level. Insects were classified into six ecological roles based on trophic habits (Fath and Killian 2007; Gobbi and Latella 2011) by literature survey (e.g. Mellini 1997; Gregor et al. 2002; Oosterbroek 2006; Jedlička et al. 2009): detritivores, parasitoids, phytophagous, pollinators, predators, and opportunists.

Data analysis

We quantified structural changes (Dunne et al. 2002a) of the plant-insect network at both local (node positions) and global (network architecture) levels along the primary succession gradient. The patterns and frequency of plant-insect interactions were represented and visualized by bipartite networks (Jordano 1987, Memmott 1999, Dormann et al. 2009). A bipartite network consists of two sets of nodes (i.e. plant species and insect functional groups) linked by a set of edges in such a way that each edge links two species belonging to different node sets. In the adjacency matrix plants were represented in the rows (= lower level in the network) and insect functional groups were represented in the columns (= upper level in the network). Link weights showed the number of insect individuals that visited the corresponding plant species. In the resulted bipartite network, the size of rectangles representing plants and insects was proportional to the relative number of visits received and made within each successional stage, respectively (Dormann et al. 2009).

In order to quantify the change in network structure along the successional gradient, we computed local indices describing nodes and global indicators of network architecture. Information about the changes in topological properties along the succession provides useful information to understand the relative importance of various functional groups and may shine a light on the dynamical consequence of network assembly.

Local (node level) indices

Weighted degree (wD_i)

In a directed and weighted network, it is the sum of weights of the links connected directly to a node. This is the most local measure and often provides a fast and simple evaluation (Jordán 2009).

Weighted topological importance index (WI_i^n)

We assume a network with undirected links where trophic effects can spread in many directions

without bias. Indirect effects can spread in both bottom-up and top-down directions and, as a result, horizontally, too (i.e. from plant to plant and from insect to insect). We use WI_i^n as the topological importance of species *i* for plant-insect network with weighted links when effects "up to" *n* steps are considered as

$$\mathrm{WI}_i^n = \frac{\sum_{\mathrm{m}=1}^{n} \sigma_{\mathrm{m,i}}}{n} = \frac{\sum_{\mathrm{m}=1}^{n} \sum_{\mathrm{j}=1}^{N} a_{\mathrm{m,ji}}}{n}$$

which is the sum of effects originated from species *i* up tp *n* steps averaged over by the maximum number of steps considered (*n*). By this index, it is possible to quantify the internal interactions structure of the network (Jordán 2009).

Both *wD* and WI^n were calculated according to Valentini and Jordán (2010). These structural importance indices assume that well-connected nodes are more important in the network in a structural and possibly also in a dynamical sense (Jordán et al. 2007, Jordán et al. 2008). As pollinators, predators and parasitoids were the consistently most abundant groups, the indices were calculated only for these.

Global (network level) indices

Density

The density of a network is the number of links divided by the maximal number of potential links. In the case of weighted networks, Wasserman and Faust (1994) suggests to use the sum of link weights instead of the number of links. Also, in the case of bipartite networks, the denominator should be *NM*, where *N* and *M* are the number of nodes in the first (plants) and in the second set (insects) of nodes, respectively. Thus, we used the following formula for our weighted and bipartite

networks:

$$d = \frac{\sum_{i=1}^{L} W_i}{N \times M}$$

where L is the number of links, W_i is the weight on the i^{th} link, N is the number of plant species and M is the number of insect functional groups.

Centralization (NCI^D)

We calculated the degree–based network centrality index (NCI^D), where degree (D) is the number of neighbours of a graph node (Wasserman and Faust 1994). Note that network centrality, expressed in percentages, is maximal (100%) if a central node is directly connected to all other nodes and there is no other link in the network (i.e. a perfect star-shape), and it is minimal (0%) if the positions of all nodes are topologically equal (i.e. a lattice).

3. Results

A total of 911 insects specimens belonging to 40 families and 6 functional groups were sampled. The *L. alpina* anthophilous insect community was dominated by pollinators (84%), predators (9%) and opportunists (5%); phytophagous and detritivores both accounted for 1%. The *S. bryoides* insect community was composed of pollinators (59%), followed by parasitoids (15%), opportunists (14%), predators (8%); phytophagous and detritivores made up 3% and 1%, respectively.

Plant-anthophilous insect bipartite network

Pollinators dominated the insect community of the debris-covered glacier (stage 0) as well as of

197 stages I and II (Fig. 2). In stage III, the insect community was more diverse and structured, as
198 opportunists, parasitoids and predators increased particularly on *S. bryoides* flowers. On the oldest
199 terrain in stage IV, the insect community on *L. alpina* was still mainly represented by pollinators,
200 while *S. bryoides* showed a more functionally diverse insect community (Fig. 2). In this late-
201 successional stage, *S. bryoides* interacted mainly with parasitoids, while opportunists and predators
202 increased their frequency and pollinators became relatively less abundant (Fig. 2).
203
204 *Network indices*
205 *L. alpina* had higher *wD* in stage 0, and among all other stages no evident trend coherent with the
206 successional gradient emerged (Fig. 3a). The WI^2 of *L. alpina* generally increased from stage 0 to
207 IV, with a major change between stage II and stage III (Fig. 3b). The *wD* of *S. bryoides* increased
208 from stage 0 to II, where it reached the maximum and later decreased to stage IV (Fig. 3c). The WI^2
209 of *S. bryoides* increased from stage 0 to III, then weakly decreased in stage IV (Fig. 3d).
210 The *wD* of pollinators tended to decrease along the primary succession gradient towards earlier
211 deglaciation (Fig. 4a), whereas WI^2 of pollinators increased with later successional stages (Fig. 4b).
212 The *wD* and WI^2 of predators increased from stage 0 to IV (Fig. 4c), with a major change between
213 stage III and IV (Fig. 4d). The *wD* and WI^2 of parasitoids remained low during the early and mid
214 successional stages, then increased mainly from stage III to IV (Fig. 4e-f). Pollinators had, on
215 average, higher *wD* and WI^2 compared to predators and parasitoids.
216 Regarding the network-level properties, link density (*d*) increased (Fig. 5a) while network
217 centralisation (NCI^D) decreased with increasing successional stage (Fig. 5b). This means that the
218 various species and functional groups in the community developed more and more interactions
219 among themselves and became more and more connected, while their relative importance became
220 less heterogeneous with more equally distributed importance among them.
221

4. Discussion

Our study represents one of the first applications of bipartite network centrality analysis to the study of ecological succession. The key finding of our work is that, during succession, the importance of different insect ecological groups and the global network structure changed. Plant-anthophilous insect interactions changed from a network dominated by pollinators to a functionally more diversified food web, where the density of interactions increased while the network became decentralized and homogeneous. We hypothesize that such process may increase the robustness of the network against the local extinction of species, providing new insight into the relationship between structure and dynamic in ecological networks.

Plant-anthophilous insect bipartite network

L. alpina interacted mainly with pollinators, which were the dominant insect group along the entire successional gradient studied here. In contrast, *S. bryoides* interacted with a wider ecological spectrum where pollinators were not the dominant group along the whole successional gradient. Difference in the ecological role of anthophilous insects between plant species may be due to the presence of floral nectaries in *S. bryoides* but not in *L. alpina*, suggesting that more insect ecological roles may benefit from this sugar resource. In the *S. bryoides* community pollinators remained the dominant group during the early and mid successional stages, whereas in the late successional stage parasitoids, predators and opportunists strongly increased and pollinators decreased.

Albeit our study does not allow the inference of direct trophic relationship among insects, it may be possible that the relative decrease of pollinators is linked to the increase in predators (Raso et al. 2014) and parasitoids with the succession proceeding. Indeed, a mature ecosystem, found at the late successional stages showing high plant productivity and community diversity (Gobbi et al. 2010),

may boost more parasitoids and predators that will interact with pollinators. By meaning of bipartite networks dynamically linked we showed for the first time how different insect ecological groups are assembled and differentially interact with plants along an ecological succession gradient.

Local (node) structural changes

Weighted centrality indices of *L. alpina* showed contrasting trends. Although no clear variation emerged in *wD*, the increase in WI^2 indicates that, even if the number of direct links may not vary, indirect effects became more important with later successional stages. Highest values of the two topological indices at the successional stages II and III for *S. bryoides* indicated a more important structural position (rich interaction structure) at the intermediate successional stages. This corresponds with the abundance distribution of this species along the successional gradient, suggesting a relationship between the species environmental requirement (i.e. the species niche) and its importance in structuring the network.

With succession proceeding, pollinator *wD* decreased and that of predators and parasitoids increased: these opposite trends indicate a change in positional importance from a local to a mesoscale view (Jordán 2009). Due to different roles of species in the network (Jordán 2009), changes in their relative importance along the successional gradient causes structural changes in the network architecture. This local change may influence the global dynamic of plant-anthophilous insect interaction network, which is varying from a pollination-driven system to a more complex ecological network. In other words, the plant-anthophilous insect interactions change along the successional gradient from predominantly mutualistic interactions to a diverse set of interactions including mutualism, parasitism and predation.

Indirect effects play an important role in governing ecosystem dynamics (Jordán et al. 2008). The consistent increase in WI^2 indices for all insect ecological roles makes them more functionally important along the primary succession gradient. The importance of nodes is therefore likely to be

determined by the interaction between insect functional role type and community features along the primary succession gradient, the later mainly represented by the increase in plant species diversity and ecosystem productivity (Gobbi et al. 2010).

Thus, the use of centrality indices highlights the link in the assembly process of plant and related anthophilous insect communities and the functioning of this interaction system. Our study showed that the local importance of insect ecological roles changed within as well as among the groups along the succession gradient, suggesting a role in the dynamic of global network properties.

Global (network) structural changes

Our results show that with succession proceeding more and more links among plants and insects are formed. This may be due to the effect of time: directly, by increasing the interaction probability among the species pool, and indirectly, as a consequence of a more structured and diversified network that lastly enhances trait matching and complementarity (Vázquez et al. 2009) between plants and anthophilous insects. Furthermore, link density is affected by network dimension (Dormann et al. 2009), the latter being a consequence, in our study system, of the increase in insect abundance and plant community maturity. The increase in link density with proceeding succession is in accordance with Albrecht et al. (2010) who found an increase in the unweighted number of links per species along the Morteratsch glacier foreland (Switzerland). As link density is an indicator of complexity (May 1973), the increase of network complexity along the primary succession gradient confers stability and robustness against potential local species losses (Montoya et al. 2006) because highly connected networks will tend to be more robust to stochastic removal of nodes (Dunne et al. 2002b). Conversely, a very densely connected network is more vulnerable to species invasion as a perturbation is more likely to spread rapidly (Scheffer et al. 2012).

Patchy pioneer communities in early successional stages are highly centralised, with few nodes playing a key role while most nodes occupy peripheral positions. Throughout the primary

succession the network became de-centralised, as all nodes are connected with a similar number of links. This highlights a gradient towards a more homogeneous structural organisation: the network architecture shifts from a star-like network, where few central nodes have many connections, to a lattice-like network with no central nodes but a balanced number of edges per node (Wassermann & Faust 1994). The network de-centralisation may emerge from the decrease in direct structural importance of pollinators and the parallel increase in importance of parasitoids and predators towards later successional stages. As reported in others studies on pollination and mutualistic networks (Olesen et al. 2007, Bascompte and Stouffer 2009, Pocock et al. 2012), low interaction richness makes a network less cohesive, thus making the network more vulnerable to the removal of nodes. Thus, we could hypothesise that the observed network de-centralisation may increase the local extinction risk of species, especially in a global warming context causing glacier retreat.

In summary, considering simultaneously all the global network properties, the network shows increasing link density and increasing de-centralisation during primary succession. These two assembly processes appear to confer two contrasting properties: the former may lead to network robustness against local species extinctions whereas the latter may confer the opposite feature. Indeed, as some simulation studies suggested (Bascompte & Stouffer 2009, Pocock et al. 2012), a cohesive organization make the network more robust and stable. In our study system, probably the outcome is a balance between these two functions (i.e. increase in link density and decrease in centralisation) and the importance of species getting extinct (i.e. the species ecological group and their structural role within the network). More studies are require to understand the dynamic consequence of network structural evolution along primary succession gradients; however, our application of local and global centrality indices has proved to give important insights into these processes and their consequences.

Conclusion

We shed light on dynamically linked ecological networks in a natural time-sequence succession. Although in our study we analysed the anthophilous insect network of two ubiquitous plant species, we believe that the emerged trends may also be extended to a wider community-level pattern. New insight was provided into the initial steps of plant–insect network assembly and new light was shed on the relationship between structure and dynamic in network ecology. In conclusion, our framework highlighted the relevance of combining ecological trait and network theory to increase the link between community structure, network assembly and ecosystem functioning. Indeed, by applying network theory we will move away from pairwise comparisons and start searching for the existence of network-wide patterns of species dependence (Ings et al. 2009). We emphasize that, in the present context of climate and environmental changes, network analysis of primary succession gradients by meaning of bipartite networks and centrality indices may provide a useful framework also for the management of endangered habitat and species.

Acknowledgements

We thank the Adamello-Brenta Natural Park for providing sampling permission and subsidized accommodation. We are grateful to Giuseppe Marano and Patrizia Boracchi for their help in R programming, to Roberto Seppi for providing the glacier foreland chronology, to Chiara Compostella for providing the GIS cartography of the study area, and to the following taxonomic specialists for help with the species identification: Daniele Avesani (Diptera) and Daniele Sommaggio (Diptera), Adriano Zanetti (Coleoptera), Maurizio Pavesi (Hymenoptera). We thank Christian Schöb, the editor (Brian D. Fath) and two anonymous reviewers for fruitful comments to the first draft of the manuscript.

References

Abrams, P. A., Menge, B. A., Mittelbach, G. G., Spiller. D. A., Yodzis, P. 1996. The role of indirect

effects in food webs. In: Polis, G. A. and Winemiller, K. O. (eds.) Food webs: integration of patterns and dynamics. Chapman and Hall, London. pp. 371-395.

Albrecht, M., Riesen, M., Schmid, B. 2010. Plant-pollinator network assembly along the chronosequence of a glacier foreland. *Oikos*, **119**, 1610-1624.

Bascompte, J. 2009. Disentangling the web of life. *Science*, **325**, 416-419.

Bascompte, J. & Stouffer, D.B., 2009. The assembly and disassembly of ecological networks. *Phil. Trans. R. Soc. B*, **364**, 1781-1787.

Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., Cerabolini, B. 2006. The functional basis of a primary succession resolved by CSR classification. *Oikos*, **112**, 10-20.

Fath, B.D., Scharler, U.M., Ulanowicz, R.E., Hannon, B. 2007. Ecological network analysis: network construction. *Ecological Modelling*, **208**, 49-55.

Fath, B.D., Killian, M.C. 2007. The relevance of ecological pyramids in community assemblages. *Ecological Modelling*, **208**, 286-294.

Dormann, C.F., Fründ, J., Blüthgen, N., Gruber B. 2009. Indices, Graphs, and Null Models: Analyzing Bipartite Ecological Networks. *The Open Ecology Journal*, 2009, **2**, 7-24.

Dunne, J.A., Williams, R.J., Martinez, N.D. 2002a. Food-web structure and network theory: the role of connectance and size. *PNAS*, **99**, 12917-12922.

Dunne, J.A., Williams, R.J. and Martinez, N.D. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, **5**, 558-567.

Foster, B.L., Tilman, D. 2000. Dynamic and static view of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology*, **146**, 1-10.

Gobbi, M., De Bernardi, F., Pelfini, M., Rossaro, B., Brandmayr, P. 2006. Epigean arthropod succession along a 154 year glacier foreland chronosequence in the Forni Valley (Central Italian Alps). *Artic, Antarctic, and Alpine Research*, **38**, 357-362.

Gobbi, M., Caccianiga, M., Cerabolini, B., Luzzaro, A., De Bernardi, F. 2010. Plant adaptive

response during primary succession are associated with functional adaptations in ground beetles on deglaciated terrain. *Community Ecology*, **11**, 223-231.

Gobbi, M., Latella, L. 2011. *La fauna dei prati -1: tassonomia, ecologia e metodi di studio dei principali gruppi di invertebrati terrestri italiani.* Quaderni del Museo delle Scienze, Trento.

Gregor, F., Rozkošny, R., Barták, M., Vaňhara, J. 2002. The Muscidae (Diptera) of Central Europe. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia*.**107**,1-280.

Hodkinson, I.D., Coulson, S.J., Harrison, J., Webb, N.R. 2001. What a wonderful web they weave spiders, nutrient capture and early ecosystem development in the high Arctic – some counter-intuitive ideas on community assembly. *Oikos*, **95**, 349-352.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H., Woodward, G. 2009. Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253-269.

Jedlička, L., Kúdela, M., Stloukalová, V. (2009) *Cheklist of Diptera of the Czech Republic and Slovakia*. Electronic version 2. http://zoology.fns.uniba.sk/diptera2009

Jordán, F., Benedek, Z., Podani, J. 2007. Quantifying positional importance in food webs: A comparison of centrality indices. *Ecological Modelling*, **205**, 270-275.

Jordán, F., Okey, T.A., Bauer, B., Libralato, S. 2008. Identifying important species: Linking structure and function in ecological networks. *Ecological Modelling*, **216**, 75-80.

Jordán, F. 2009. Keystone species and food web. *Phil. Trans. R. Soc. B*, **364**, 1733-1741.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependences, asymmetries and coevolution. *American Naturalist*, **129**, 657-677.

Kaufmann, R. 2001. Invertebrate succession on an Alpine glacier foreland. *Ecology*, **82**, 2261-2278.

Matthews, J.A. 1992. *The Ecology of Recently-deglaciated Terrain: A Geoecological Approach to*

397 *Glacier Forelands and Primary Succession.* Cambridge University Press, Cambridge.
398 May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press,
399 Princeton.
400 Mellini, E. 1997. From predation to parassitoidism in the Diptera order. *Bollettino dell'Istituto di*
401 *Entomologia "Guido Grandi" della Università degli Studi di Bologna*, **51**, 91-159.
402 Memmott, J. 1999. The structure of a plant-pollinator food web. *Ecology Letters*, **2**, 276-280.
403 Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and
404 importance. *Ecological Monographs*, **65**, 21-74.
405 Montoya, J.M., Pimm, S.L., Solé, R.V. 2006. Ecological networks and their fragility. *Nature*, **442**,
406 259-264.
407 Pascual, M., Dunne, J.A. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs.*
408 Santa Fe Institute, Studies in the Sciences of Complexity. Oxford University Press, Oxford.
409 Olesen, J., Bascompte, J., Dupont, Y., Jordano, P. 2007. The modularity of pollination network.
410 *PNAS*, **104**, 19891-19896.
411 Oosterbroek, P. 2006. *The European families of Diptera: Identification, diagnosis, biology.* KNNV
412 Publishing, Utrecht.
413 Pocock, M.J., Evans, D.M., Memmott, J. 2012. The robustness and Restoration of a Network of
414 Ecological Networks. *Science*, **335**, 973-977.
415 Raso, L., Sint, D., Mayer, R., Plangg, S., Recheis, R., Kaufmann, R., Traugott M. 2014. Intraguild
416 predation in pioneer predator communities of Alpine glacier forelands. *Molecular Ecology*, **23**,
417 3744-3754.
418 Scheffer M., Carpenter, S., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J.,
419 van de Leemput, I., Levin, S.A., van Nes, E.H., Pascual, M., Vandermeer, J. 2012. Anticipating
420 Critical Transitions. *Science*, **338**, 344-348.
421 Sridhar, H., Jordán, F., Shanker, K. 2013. Species importance in a heterospecific foraging

association network. *Oikos*, **122**, 1325-1334.

Thébault, E., Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, **329**, 853–856.

Valentini, R., Jordán, F. 2010. CoSBiLab Graph: the network analysis module of CoSBiLab. *Environmental Modelling and Software*, **25**, 886-888.

Vázquez, D., Blüthgen, N., Cagnolo, L., Chacoff, N. 2009. Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany*, **103**, 1445-1457.

Walker, L.R., del Moral, R. 2003. *Primary succession and Ecosystem Rehabilitation.* Cambridge, Cambridge University Press.

Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D. 2010. The use of chronosequence in studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725-736.

Wasserman, S., Faust, K. 1994. *Social Network Analysis: Methods and Applications.* Cambridge: Cambridge University Press.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Ann. Rev. Ecol. Syst.*, **25**, 443-466.